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SPATIAL ASPECTS OF VEGETATION DYNAMICS INDUCED BY HERBICIDE DISTURBANCES IN A HUNGARIAN LOESS GRASSLAND COMMUNITY

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Abstract. Major floristic changes induced by leaf-herbicides selective to dicots and monocots and a comprehensive leaf-herbicide in an old perennial grassland community were studied for 10 years using permanent quadrates at 3 spatial microscales (at 400 cm^2, 1 m^2 and 5 m^2 plot sizes). Great impact of spatial scale upon the detection of dynamic phenomena and recognition of recovery tendency as well as the assessment of its degree was analyzed during the local secondary microsuccessions following herbicide-disturbances.
Similarity analyses and principal coordinates ordinations were applied to measure the rate of floristic change and to reveal trends in temporal variation of species composition, variability of regenerative trajectories, as well as to estimate the degree of recovery at 400 cm^2, 1 m^2 and 5 m^2 plot sizes.
The results indicated significant differences in the variation of floristic composition and in the rate of major floristic changes at small versus larger sizes of quadrates.
It was concluded that the different changes in spatial microheterogeneity of the originally homogeneous stand of the community caused by the herbicide-disturbances strongly affected the appropriate plot size for detecting grassland recovery-dynamics. The spatial heterogeneity changes induced by the herbicides were especially critical in comparison of the different treatments as well as in assessing the degree of recovery of the treated plots to control ones.
It was stated that the observable differences between floristic pattern at different spatial scales would be the result of different degrees of spatial heterogeneity within the community.
A change of spatial scale (the size of experimental plots) brought forth, in fact, a new perception of vegetation dynamic processes and the results also highlighted different aspects of species abundance hierarchy.

Keywords: herbicide-disturbances, spatial scales, temporal floristic pattern.

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Introduction

Spatial-scale dependence of grassland dynamics as well as the influence of disturbances on different biological organization levels and at different spatial scales have been well-documented recently (e.g.: Chaneton-Facelly, 1991; Collins and Gibson, 1990; Glenn-Lewin-Ver Hoef, 1988; Hogeweg et al., 1985; Sousa, 1984; Thórhallsdóttir, 1990; White and Pickett, 1985). This field study demonstrates spatial aspects of grassland dynamics in a community which was experimentally manipulated.

Leaf herbicides selective to dicots and monocots, as well as a comprehensive herbicide were applied using permanent plots in a species rich old perennial grassland community in Hungary to induce quick vegetation dynamic processes (Virágh, 1982). Major floristic and structural changes during secondary successions and regeneration capability of the community after herbicide disturbances were studied. Using herbicides as disturbance agents was very useful also from practical point of view. At present application of herbicides in sward-farming is a fairly general method for removal of weeds and for improvement of the sward (selective extirpation), as well as for total destruction of the vegetation in order to re-new, re-sow the sward. So some questions mostly regarding recovery, important in my experiments, must be very important for practice and cannot be answered without taking the vegetation and population dynamic processes into account.

At a local scale my controlled disturbance experiments aimed to study the endogenous dynamics, temporal floristic fluctuation of a relatively intact loess steppe grassland community for a long time period and to examine how natural ⁴ man-made disturbances impact the species composition and dynamic behaviour (resistance, recovery) of the studied community. Population dynamics, community regenerative and secondary microsuccessional processes following herbicide treatments of different types, intensity and frequency were analyzed for 10 years. The effect of herbicide treatments on the cenological similarity relations, as well as the utility of different resemblance indices and multivariate analyses in detecting vegetation temporal changes were reported by Virágh (1987a). The degree of community-recovery after disturbances and its resistance against drought were assessed by comparing control plots and herbicide-disturbed plots with respect to major floristic changes (Virágh, 1986; 1987a; 1987b), some textural and structural community attributes (Virágh, 1989a; 1991) and recovery patterns of populations (Virágh, 1989b). Determination of buried viable seed populations in the soil (Virágh and Gerencsér, 1989) was also included in the investigation.

In vegetation dynamic studies examining the effect of herbicide treatments, the selection of methods is critical. The result of methodological studies has been discussed in a previous article (Virágh, 1987b). In addition, due to the different effects of herbicides, choosing the appropriate size of experimental plots for comparing many treatments and for measuring the degree of recovery is also a very crucial point. The problems are the following:

The herbicides used caused different changes in microheterogeneity of the originally homogeneous stand. They altered the species hierarchy by changing the rank order of some previously dominant species and increasing the relative importance of subordinate species (Virágh, 1989a).

Selective herbicides, which killed the dicots represented by many species but with low abundance and the other killed the dominant and most abundant monocots, significantly changed the abundance-dominance relations among the species. The herbicides also produced smaller and larger bare-ground surfaces in different numbers, causing local spatial microheterogeneity differences in the study area. Later these topographical differences due to the herbicide-disturbances, could also increase with time because of the differential growth of surviving populations as well as the differential rate and manner of colonizations with various first colonizers.

So analyzing the impact of spatial scales applied upon the recognition of dynamic phenomena was significant in the differently disturbed community.

This paper analyses the temporal variation of species composition at 3 spatial microscales (at 3 plot sizes) and the effect of size of sampling plots on detection of recovery tendency. The significance of appropriate size of investigated plots in the comparison of the differently disturbed community for detecting community-recovery and measuring its degree is mainly emphasized here.

The study aims to answer to following questions:

1) How different view on dynamic phenomena (direction and rate of floristic change, the degree of responses to drought) and dynamic processes (seasonal dynamics and recovery) may be obtained by similarity analyses at different plot sizes in the intact and herbicide-treated community?

2) What is the effect of spatial sample-scales on temporal floristic patterns in the principal coordinates ordination space and the classification space?

3) What size of sampling plots can be acceptable for detecting grassland recovery in this differently disturbed community?

Material and Methods

Field experiments

Field study was carried out on a dry-situated hill, at the southern foot of the Bükk Mountains (NE-Hungary), about 200-300 m above sea level in Hungary. The mean annual temperature is 9 °C, the total precipitation is about 600 mm. The soil is brown forest soil of chernozem character, formed on loess. The study area is in a secondary steppe community: *Pulsatillo-Festucetum rupicolae*, formed a very long time ago in place of deforestation. It can be considered as the final stage (subclimax community) in a successional series of grasslands in the given area. Detailed description of this community and the sources of richness of flora are presented in previous papers: Virágh (1982) and

Virágh and Fekete (1984).

The research program was launched in 1979 and the experiments ran for 10 years in a fairly stable *Pulsatillo-Festucetum rupicolae* community. A homogeneous stand of this species rich community was selected for studies of local secondary succession, i.e., regeneration processes initiated by some herbicide treatments (Virágh, 1982; 1986).

The experiments carried out are briefly summarized bellow:

CONTROL experiment.

It represents vegetational changes without any treatment.

GABONIL experiment (4 l/ha dose, 7 l/ha dose)

Gabonil: MCPA+dicamba:

4-chloro-2-methyl phenoxyacetic acid+2-methoxy-3.6-dichloro-benzoic acid

The dicots, the less dominant group, were killed. Immediately after spraying, there was a possibility for expansion of grasses and later for the re-settlement of some dicots.

DALAPON experiment (12 kg/ha dose, 20 kg/ha dose)

Dalapon: 2.2-dichloropropionic acid

The dominant monocots were killed leading to large spots of bare ground on which some dicots well spreading by vegetative propagula became predominant and determined subsequent vegetation changes.

The monocots reappeared some years later.

GLYPHOSATE experiment (15 kg/ha)

Glyphosate:4-(phosphono-methyl)glycine

All the vegetation was killed. The bare ground was particularly recolonized from seeds and from the sedge by vegetative propagula. The secondary succession was mainly determined by the first colonizers.

It must be noted that the leaf herbicides used did not cause habitat changes or ground-surface changes in the field. They were applied in a relatively small plots of 1.5x1.5 m. The processes taking place in the small windows were governed by the surrounding vegetation. Thus, during the period of 10 years of study there was no succession in the general sense of the word, that is the sense of substitution of well-defined communities by others. As a consequence of the direct effects of herbicides, after the partial or complete killing of the vegetation, smaller and larger bare-ground surfaces appeared in the stand. These different types of localized secondary microsuccessions and regeneration processes were initiated. Only the species previously present in the community returned. But the development of vegetation proceeded step by step by the replacement of different well-defined coenostates.

Sampling

The experiments were arranged in a randomized block design with 5 replications per treatment. The field investigations were carried out twice a year in 1 m^2 permanent plots with 5 replications, covered with a grid of 4x4 cm, as well as 20x20 cm units. Presence - absence and percentage cover of each species, visually estimated, were mainly recorded in a set of 400 cm^2 contagious subquadrates (125 in total per treatment) and then the cover values were summed for 1 m^2 and 5 m^2 quadrates in each experiment.

Remarks on the relevant plot sizes

-- Maximum value of the cover-based significant ISC and aggregation sums of most of the species was apparent at 400 cm^2 plot size on the study-site. The number of species combination was also the highest and the stand proved to be the most heterogeneous at this characteristic area for the most abundant species. The floristic changes on this spatial microscale indicated the effect of herbicides very sensitively.

-- At 1 m^2 plot size summation of the smaller scale dynamics was manifested. Variability among these plots, resulted from the plots differed in species composition and abundance, reflected the local spatial heterogeneity, characteristic for the whole stand.

-- Considering all of the species, the 5 m^2 size of plots contained a portion of the stand large enough to be floristically homogeneous and characteristic for the whole stand.

The area was sprayed at one occasion at the end of June, but the treatment by the two selective herbicides of larger dose was repeated again after a year. Dates of spraying were: June 1979, and June 1980, respectively.

The investigations were performed from 1979 to 1989. Floristic composition of treated quadrates was recorded before and after the treatments in June and in September from 1979 to 1983 and then 1987 and 1989. The control plots were also examined twice a year.

Data

The presence-absence and cover-scores were summarized in a species by quadrates data matrix (400 cm^2, 1 m^2, 5 m^2) for each point of time and each treatment. Such a matrix represents the operational unit (basic object) of multivariate analyses. To facilitate the use of resemblance coefficients for comparing points of time, these matrices were often transformed into vector form. Consequently, in these cases only the temporal change within subquadrates or quadrates is manifested in the final results, and here the variation between the replicate plots does not influence similarity analyses, ordinations and classifications.

Methods

1) Similarity indices were used to analyze the effects of treatment and plot size on

a) the cenological similarity relations
b) the direction of secondary successions,
c) the rates of change,
d) the degree of community recovery,
e) the seasonal dynamics and
f) the responses to drought.

The year to year changes, as well as the changes referring to the first point of sampling date, namely the trend of changes during the investigated period were analyzed. Similarities between consecutive points of time, as well as similarities between each of the points of time and the initial sample time were calculated here by Sørensen index and Czekanowski's percentage similarity coefficient. These indices proved to be the most appropriate for revealing similarity relations involved in floristic data matrices (see Virágh, 1987a; 1987b).

The rates of change were calculated as floristic change and as cover-based change also by means of the two similarity indices mentioned earlier. These were suggested by Bornkamm (1981) and Armesto and Pickett (1986) for determining rates and magnitudes of vegetational changes.

Two referenced states were accepted for my comparative analyses:

a) pre-disturbed floristic state in every treatment and

b) control dynamics, the intact natural condition including normal temporal changes.

The value of similarity indices could indicate the degree of community-recovery to the original pre-disturbed or to the control compositional state.

The years 1982 and 1987 were dryer than usual. The effects of these extremely dry summers ("stress situation") could be measured in the deviations of values of Sørensen and Czekanowski's similarity coefficient.

2) Principal coordinates ordinations and clustering methods were applied to reveal trends in temporal variation of species composition and variability of regenerative trajectories as well as to estimate the degree of recovery at different spatial microscales (at 3 plot sizes).

3) Comparison of the dendrograms and the ordination results

a) Comparison of small and larger patterns in the same observational data set (a single experiment) was evaluated by using pairwise comparison of ordinations by Procrustes analysis (Schoenemann and Caroll, 1970; Gower, 1971, 1975; Sibson, 1978) and of classifications by using 7 coefficients (Podani , 1984).

b) The method of multiple comparison of classifications (Podani, 1982; Podani and Dickinson, 1984) of cover data of different data sets, originated from various treatments, was also used to reveal similarity relationships among the dendrograms obtained at different spatial scales and to examine the relative impact of treatments and plot sizes upon the vegetation pattern.

Results and discussion

Similarity analyses at 3 plot sizes

The results of similarity analyses (Fig. 1 and 2) demonstrated the differences in the temporal variation of floristic composition and in the rate of floristic change at small versus larger sizes of quadrates. Microheterogeneity differences smooth with time so the larger size of sample-quadrates significantly reduced the floristic variation and decreased the rate of observable changes in each treatment.

The detection of grassland recovery tendency and assessment of its degree in differently disturbed communities were also strongly affected by the size of sampling plots.

While all of the 3 plots sizes (400 cm^2 , 1 m^2, 5 m^2) had nearly the same results about the trend of floristic changes in the control experiment, but great differences appear in the herbicide treatments. Only 5 m^2 quadrates prove to be sufficiently large to reveal the tendency of recovery of the plots treated by Gabonil herbicide, eliminating the subordinate dicots, but after killing of the dominant monocots convergence in the species composition of Dalapon-treated plots to the pre-disturbed compositional state appears already at 1 m^2 quadrates (see Fig. 1).

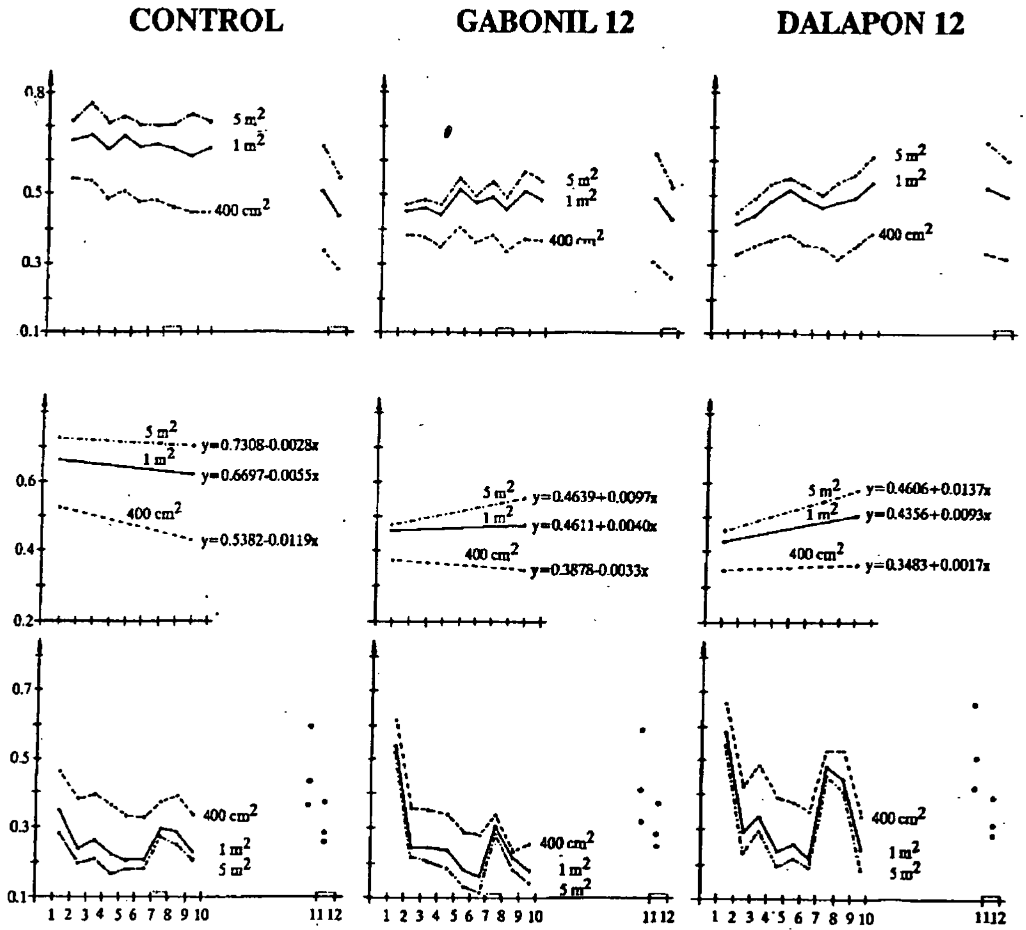


Fig. 1. Effect of plot size on the results of similarity analysis in 3 experiments. (Resemblance is measured by Czekanowski's similarity coefficient. 1: June 1979; 2: September 1979; 3: June 1980; 4: September 1980; 5: June 1981; 6: September 1981; 7: June 1982; 8: September 1982; 9: June 1983; 10: September 1983; 11: June 1987; 12: September 1987. Gabonil 4: Gabonil 4 kg/ha dose; Dalapon 12: Dalapon 12 kg/ha dose.) Upper row: trend of species cover changes (Similarities {Czekanowski index} between each of the points of time and thee initial sample time). Middle row: fitting of linear curve for cover changes. Lower row: rate of cover-based change (Dissimilarities between consecutive sample times)

The expression of seasonal dynamics was strongly decreased by increasing the size of sampling plots.

The effects of herbicides as well as the responses to drought were also dissimilarly manifested at the 3 spatial scales and they could be detected in various degree in each treatment depended on the plot sizes.

The expression of differences among the treatments was also very dissimilar at the 3 plot sizes investigated (Fig. 2). The quantitative differences (Czekanowski-index) in species composition of the treatments were significant in each size of sampling plots, however the qualitative compositional differences (Sørensen index) could especially be detected at 400 cm² quadrates and they could hardly be recognizable after 2 or 3 years following the treatments at 5 m² quadrates.

Temporal floristic pattern at 3 plot sizes. The influence of plot size on vegetation pattern in time

Grassland dynamics in the principal coordinates ordination space and the classification space

Spatial sample scales also affected the observation of temporal patterns during the 10 years of study-period (Fig. 3).

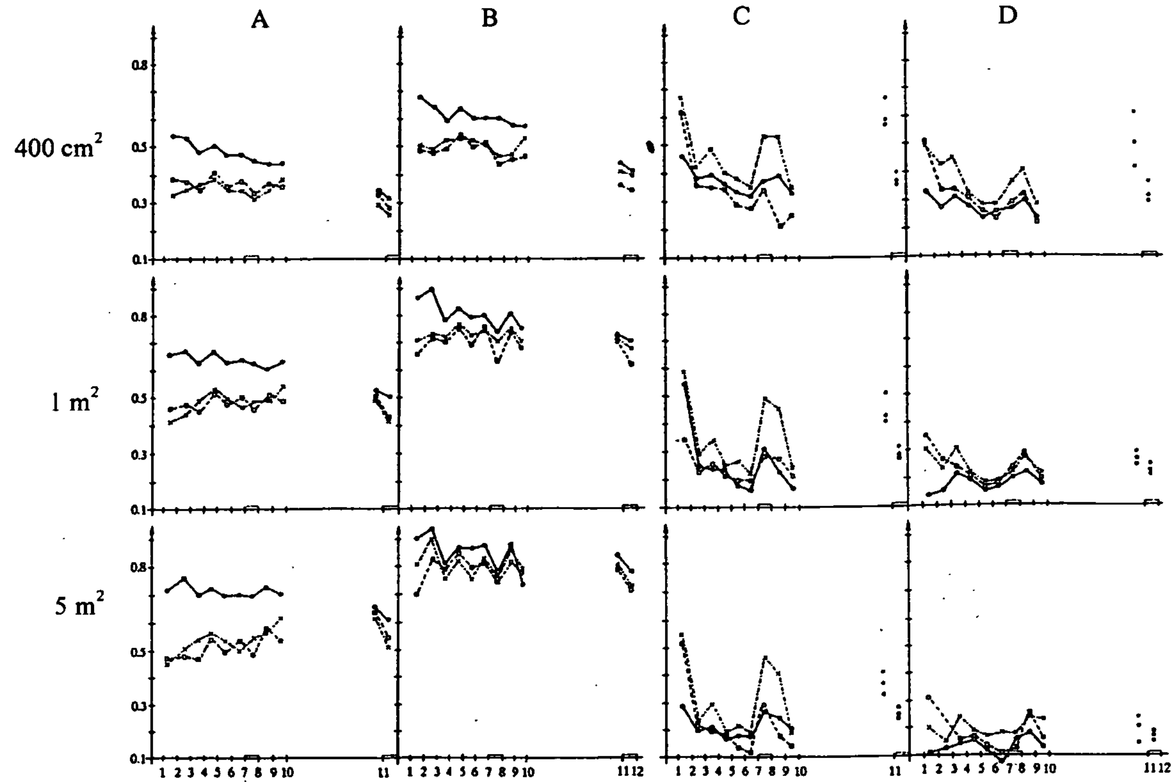


Fig. 2. Differences in trend and rate of cover-based change and floristic change between the treatments at 3 plot sizes. Trend of cover-based change [A] (Czekanowski's percentage similarity index) and of floristic change [B] (Sorensen index) and rate of cover-based change [C] (Czekanowski's percentage similarity index) and of floristic change [C] (Sorensen index); (control———, Gabonil 4 ········, Dalapon 12 –·–·–·–. See Fig. 1. for explanation of symbols and numbers.)

Pairwise comparison of ordinations of points of time (see Fig. 3) for different plot sizes reflected that the ordination results in Gabonil experiments were in a good agreement.

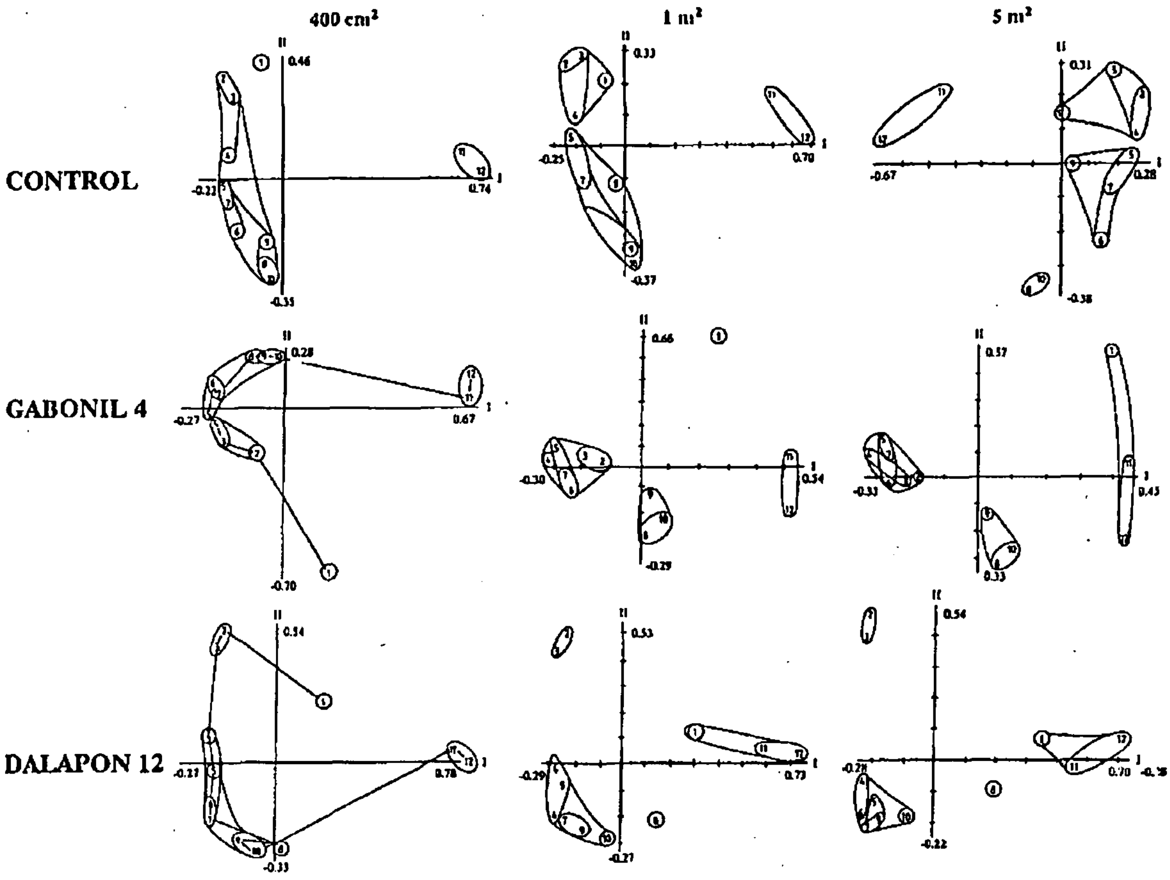
The control plots of different sizes tended to produce somewhat different ordination results, though the underlying trends in vegetation dynamics revealed were very similar. Here the results on temporal patterns were nearly the same at the 2 smaller plot sizes, but from these a more or less different pattern of points of time was detected at 5 m².

If the variation among the 5 replicates of 1 m² plots was also manifested (Fig. 4), the ordination showed that the variability among the 1 m² plots was much more considerable than that was among the points of time. In this case it may be advisable not to sum the data for 5 m² and the interpretation of recovery at population level can be only possible at 1 m² plot size.

This inconsistency among the results might occur because of the specific vegetation development of the five 1 m² quadrates probably induced by the changes in the dominance of some species.

The greatest difference was revealed between the ordinations in the case of Dalapon-treated plots. The pattern of points of time at 400 cm² plot size was strongly different from that was at the larger quadrates. The high inconsistency between the results at 3 sample-scales in this experiment might occur because of the rapid vegetative regeneration and the great expansion of some clonal dicots, indicating that the 400 cm² plots were not large enough to include the most predominant and abundant dicots after herbicide-disturbances.

The classifications also clearly showed the great impact of plot sizes on temporal vegetation pattern in each treatment (Fig. 5). The differences referring to the overall structure of dendrograms were well-reflected by the results of dendrogram-comparisons (Table 1), by which the separation of vegetation pattern of the 400 cm² Dalapon-treated plots from the others was the most strikingly expressed.



Pairvise comparison of ordinations

Procrustes analysis	sum of squares	
	400 cm^2 - 1 m^2	1 m^2 - 5 m^2
Control	0.062	0.129
Gabonil 4	0.028	0.020
Dalapon 12	0.140	0.026

Fig. 3. Effect of plot size on the result of principal coordinates ordination of points of time in 3 experiments. (Resemblance is measured by Czekanowski's similarity coefficient. See Fig. 1. for explanation of numbers.)

The effect of treatment and plot size on the classifications

When the classification results of 3 plot sizes were analyzed for all treatments simultaneously (Fig. 6), the sharp separation of Dalapon-treated plots from the control plots and Gabonil-treated ones, owing to the elimination of dominant monocots, could be well-detected. The result of multiple comparison of dendrograms also indicated that the dissimilarities in the pattern of points of time of the treatments were mainly caused by the herbicides (axis I accounted for 31% of the total variance) and by the spatial sample-scales in lesser degree (axis III: 13%).

Appropriate scale for detecting grassland recovery

The results presented earlier clearly showed that the most influential factor on the vegetation dynamics was the effect of herbicide-disturbances but all observations about the floristic changes were strongly constrained by the size of sampling plots applied. Great impact of the size of investigated plots (spatial microscales) upon the detection of dynamic phenomena and recognition of temporal floristic patterns as well as recovery tendency was well-demonstrated.

It was concluded that when the recovery of differently disturbed plots, the convergence in

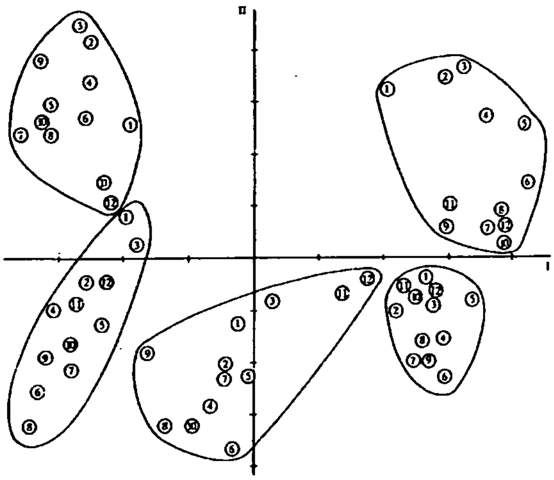


Fig. 4. Principal coordinates ordination of points of time in the case of 5 replications of 1 m^2 quadrat in the control experiment. (Resemblance is measured by Czekanowski's similarity coefficient. See Fig. 1. for explanation of numbers.)

species composition of treated plots to control ones was analyzed at community level (Fig. 7), in order to avoid the different spatial microheterogeneity effects caused by the herbicide-treatments, the results were necessarily referenced for 5 m^2 plot size, at which the summation of "patch dynamics" (microtopographical heterogeneity) would come to exist. Compositional recovery is well indicated by the result of ordination of points of time (Fig. 7).

In the comparison of 5 experiments (control and the 2 selective herbicides in 2 different doses), the ordination (Fig. 7) clearly shows homogeneity of the original community without treatments, as well as sharp distinction between the compositional temporal pattern of control and treated plots during the first 5 years of study. Relatively great impact of herbicide-doses upon the ordination results is also well-expressed. It was also apparent here that during the first 5 years the treated plots could not return to their pre-disturbed state. Despite of the results of 5 years, in the comparison of 5 treatments for 9 years, very high similarity values among the first and the last 2 coenostates (or points of sampling dates) can be well-reflected in the ordination space, indicating compositional recovery during 9 years.

Whereas, when all the vegetation was completely killed (Glyphosate experiment), the secondary succession was mainly determined by the first species occupying the bare ground. Here the 5 replications of 1 m^2 quadrate due to their differential initial composition after herbicide-disturbances were well-separated from each other (Fig. 8), indicating a specific way of vegetation development in each 1 m^2 quadrate. The five 1 m^2 Glyphosate-treated quadrates also became increasingly dissimilar floristically with time, probably due to the stochastic colonization and its differential rate and manner. So because of the strong spatial heterogeneity produced and also the specific way of vegetation development of the 1 m^2 individual quadrates induced by their various initial species composition in the very early colonization phase, it was necessary to examine floristic changes in each of the separated 1 m^2 quadrates independently.

Table 1. Dendrogram comparison by using 7 coefficients

	Descriptor	400 cm^2 - 1 m^2
Control	cladistic difference	12.65
	cophenetic difference	60.35
	cluster membership divergence	13.63
	number of changes in ultrametric relationship	31.00
	ultrametric dissimilarity	0.14
	mismatched edge difference	55.56
	absolute edge difference	200.96
	edge matching coefficient	0.50
Gabonil 4	cladistic difference	12.00
	cophenetic difference	46.33
	cluster membership divergence	17.08
	number of changes in ultrametric relationship	53.00
	ultrametric dissimilarity	0.24
	mismatched edge difference	71.39
	absolute edge difference	168.93
	edge matching coefficient	0.50
Dalapon 12	cladistic difference	14.56
	cophenetic difference	85.21
	cluster membership divergence	27.89
	number of changes in ultrametric relationship	77.00
	ultrametric dissimilarity	0.35
	mismatched edge difference	112.41
	absolute edge difference	227.99
	edge matching coefficient	0.70

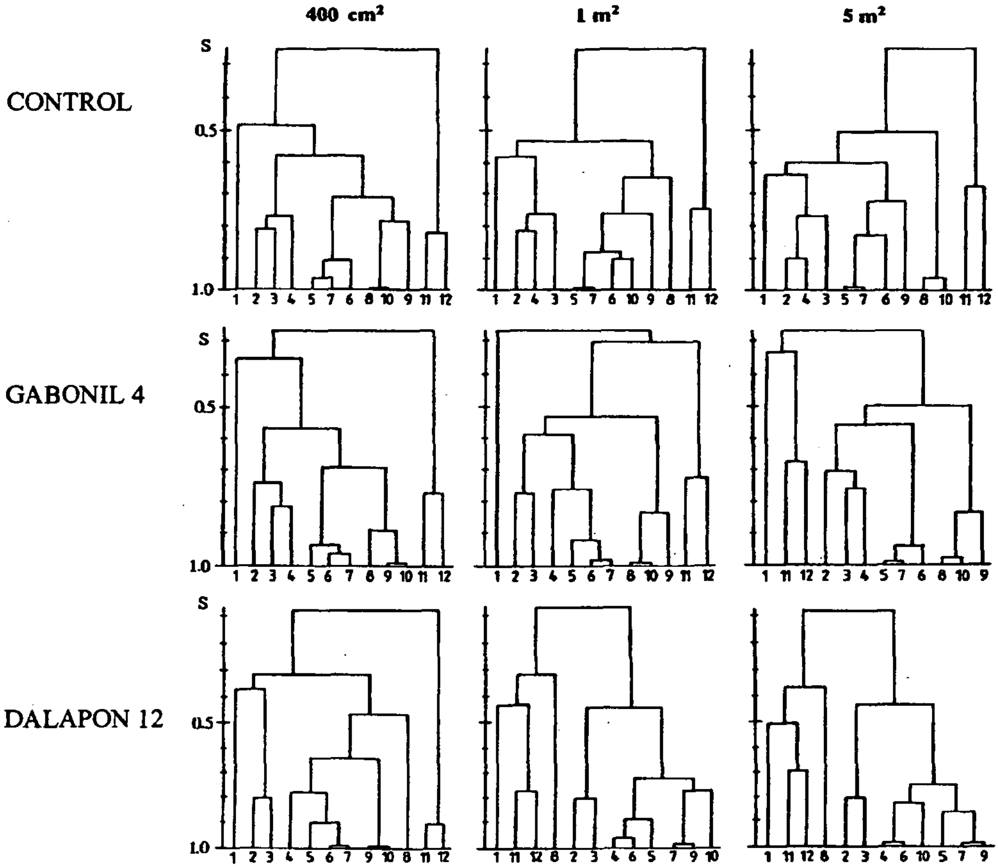
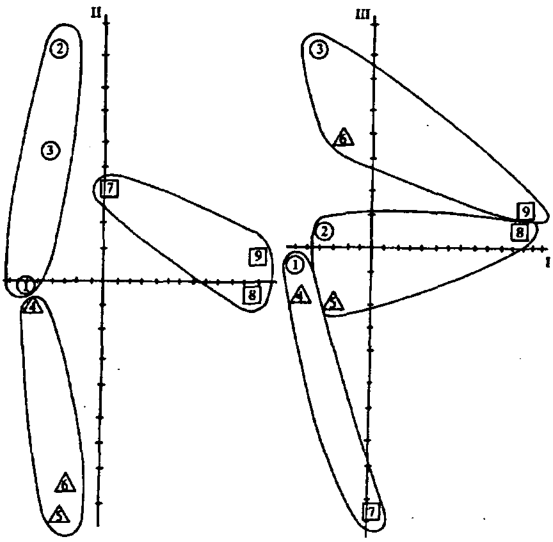


Fig. 5. Effect of plot size on the results of classification of points of time in 3 experiments. (See Fig. 1. for explanation of numbers.)



Squared distance matrix

1	2	3	4	5	6	7	8	9	
0.00	2.54	2.66	1.25	2.52	2.39	2.82	4.17	4.27	1
	0.00	2.87	2.57	4.06	3.74	3.09	4.39	4.31	2
		0.00	2.99	3.54	3.24	3.52	4.46	4.48	3
			0.00	2.6	2.44	2.84	4.15	4.30	4
				0.00	2.24	3.14	4.07	4.31	5
					0.00	3.70	3.81	4.01	6
						0.00	3.64	3.73	7
							0.00	1.46	8
								0.00	9

Symbols used in ordinations	400 cm^2	1 m^2	5 m^2
Control	1	2	3
Gabonil 4	4	5	6
Dalapon 12	7	8	9

Fig. 6. Effect of treatment and plot size on the classifications. Principal coordinates ordination of classifications of 3 treatments at 3 plot sizes. (Resemblance is measured by Czekanowski's similarity coefficient.)

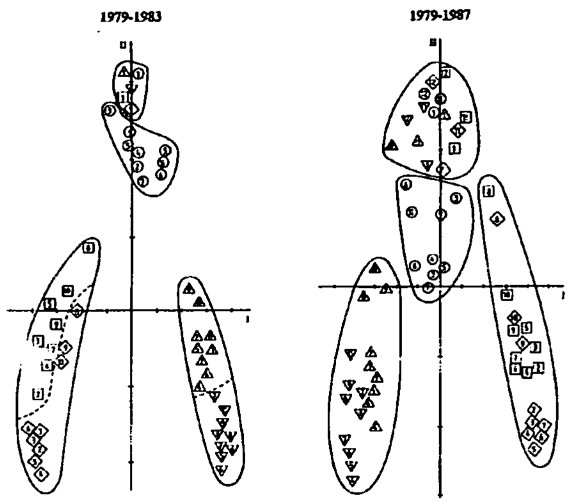


Fig. 7. Principal coordinates ordination of points of time of 5 treatments (control ○, Gabonil 4 △, Gabonil 7 ▽, Dalapon 12 □, Dalapon 20 ◇. Resemblance is measured by Czekanowski's similarity coefficient. See Fig. 1. for explanation of numbers.)

Concluding remarks

It was obvious that different changes in spatial microheterogeneity of the originally homogeneous stand of the community caused by the herbicide-disturbances were very important for interpreting the synmorphological phenomena and dynamic processes during the localized secondary microsuccessions.

The results of comparative analyses based on cenological similarities proved the great importance of the size of investigated quadrates chosen for detecting grassland recovery dynamics and supported the view that the recognition of vegetation dynamic processes is inherently spatial-scale dependent.

The results also suggested that it is likely that the differences observed between floristic patterns at the different spatial scales (microscale: 400 cm^2, local patch-scale: 1 m^2, stand-scale: 5 m^2) might be the result of different effects of herbicide-disturbances and various degrees of spatial heterogeneity induced by herbicide treatments within the community.

It seems very possible that the relative importance of both deterministic and stochastic influential factors on floristic change also varied with spatial scale. Beside the herbicide effects, patterns on the smallest plot size were mainly determined by the spacing, interacting and size of individual plants. In contrast, patterns on larger scales were most influenced by the competitive interactions of the constituting species following disturbances and the local environmental factors.

These descriptive analyses yielded meaningful results on the temporal pattern of major floristic changes at community level. A change of spatial scale brought forth, in fact, a new perception of vegetation dynamic processes. However, it is also obvious, that many questions remain open and additional statistical tests and studies on population dynamics (Virágh, 1989) of the species are necessary. Detailed investigations of species

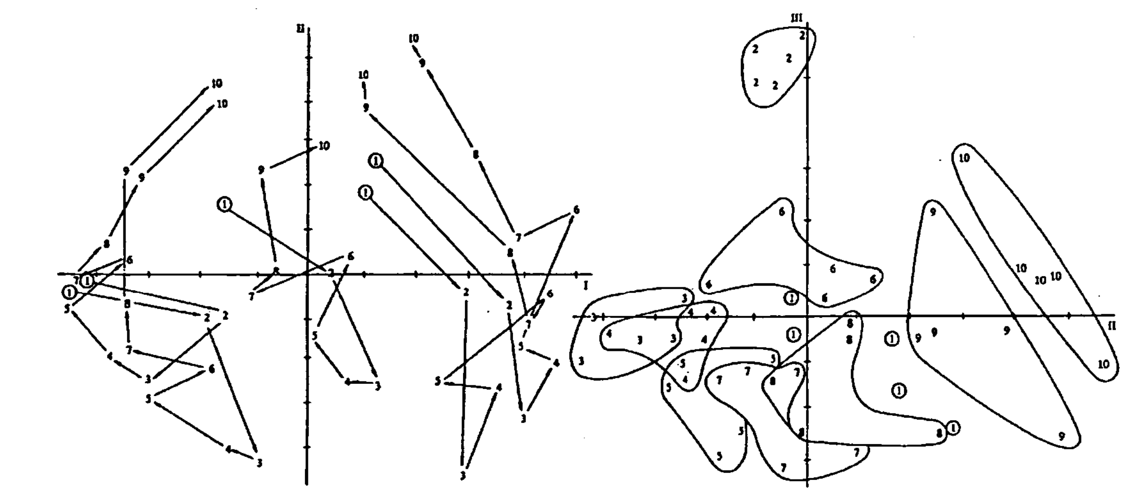


Fig. 8. Principal coordinates ordination of points of time in the case of 5 replications of 1 m^2 quadrat in the Glyphosate experiment. (Resemblance is measured by Czekanowski's similarity coefficient. See Fig. 1. for explanation of numbers.)

distributions and pattern abundance-dominance relationships by changing the size of study-area are also needed for understanding community changes and their appropriate interpretation at different spatial scales.

This is a preliminary experiment, which can be used later for generating some hypotheses. However, the results of this experiment can be useful for researchers who are further using herbicides or learning their effect.

Acknowledgements

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